THE GROWTH-FORMS OF THE FLORA OF NEW YORK AND VICINITY[1]

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There has recently appeared in a work on the flora of New York,[2] an account of the relation between climate and the vegetation in which the length of the growing season was used as the chief temperature factor. This was done for the reason that it seemed to account for the distribution of the flora more closely than any other ascertainable temperature factor. While it is difficult to conceive of any climatic agency, such as the number of frostless days, the maximum or minimum temperatures, or the accumulated heat units, as actually controlling the distribution of the flora, yet it is a matter of common observation that temperature does affect vegetation and its distribution. How, then, are we to measure the effect of climate, and particularly temperature, on plant life? All of the older methods, including the one used in the flora of the vicinity of New York, have studied climate as a rather distinct entity, and then imposed a somewhat rigid, usually instrumentally correct scheme, on a complex aggregate like a local flora. All such schemes require considerable wrenching of the purely climatic factors on the one hand, as they certainly do of the assumed vegetative response on the other. Until recently, and with the possible exception of Merriam's "Life Zones," all studies of the effect of temperature on plants were of this type. They were essentially attempts to explain the facts of plant distribution by measured temperatures or heat units or frostless days or by some combination of these methods.

Raunkiaer[3] has studied temperature factors from an entirely different viewpoint. His idea, briefly, is that we must study climate,

[1] Brooklyn Botanic Garden Contributions, No. 9.

[2] Taylor, N. Flora of the vicinity of New York: A contribution to plant geography. Mem. N. Y. Bot. Garden 5: 1–683. 1915. See pp. 33–36. All the statistics and figures used in this paper may be verified in that book. The nomenclature of the present paper is essentially that of the Gray's Manual.

[3] A fairly complete account of Raunkiaer's system, with a bibliography, may be found in Journ. Ecol. 1: 16–26. 1913.

not as such, but as it is reflected in the vegetation which we all know it to have controlled. Such a method is not at all in line with older studies, it is really an *ex post facto* method of determining climate by the character of the vegetative response. From the standpoint of the ecologist and plant geographer, what could be more logical and reasonable? Temperature factors are not what one makes them out to be with an elaborate instrumental or mathematical method; they are rather what one finds them as reflected in the vegetation itself. Of course, in order to get the quality and kind of this implied vegetative response, we must study plants in a slightly new light, and Raunkiaer has devised, after Warming and a few earlier writers, a scheme for such a study.

His theory is that plants react to climate by the kind and amount of protection exhibited by the perennating growth points during the winter or critical season. Upon this assumption he divides all vegetation into several different groups of growth-forms sometimes called life-forms, depending on the kind and amount of protection to their growing buds exhibited by each. In the following account, I have included only those of his growth-forms that are found in eastern North America, which may be characterized as follows:

Phanerophytes. Woody plants of all types, both evergreen and deciduous and exhibiting the least amount of protection from the cold, as showing the greatest amount of exposure. The group may be divided into **Megaphanerophytes,** trees over 30 m.; **Mesaphanerophytes,** trees 8–30 m.; **Microphanerophytes,** shrubs or trees 2–8 m.; **Nanophanerophytes.** shrubs under 2 m. Examples of all these are too common to need citing.

Chamaephytes. Perennial by virtue of the fact that the buds are just above the ground, or on the surface, and are thus often protected by the snow blanket. Among local species *Arctostaphylos Uva-Ursi*, *Epigaea*, *Convolvulus*, etc., are good examples. It includes, also, cushion-plants.

Hemicryptophytes. With dormant buds in the upper crust of the soil, the top of the plant dying down in the winter. Common examples suggest themselves, as all our shallow-rooted herbaceous perennials belong here.

Geophytes. Perennial by bulbs, rhizomes, tubers or by root-buds. Examples among our native plants: most Orchidaceae, Liliaceae, *Sanguinaria*, *Hydrastis*, etc.

Helophytes and Hydrophytes. The former has buds at the bottom of the water. They are mostly marsh species such as *Typha*, *Sparganium*, *Acorus*, etc. Hydrophytes have perennating rhizomes or winter-buds and are truly aquatic, such as *Castalia*, *Elodea* and *Potamogeton*.

Therophytes. Annuals.

A tabular view of these different growth forms, with the abbreviations as used in this paper follows:

MG = Megaphanerophytes	CH = Chamaephytes
MS = Mesaphanerophytes	H = Hemicryptophytes
MC = Microphanerophytes	G = Geophytes
N = Nanophanerophytes	HH = Helophytes and Hydrophytes
	T = Therophytes

Raunkiaer's method of adapting the study of these growth-forms as related to temperature is to estimate the number of species characterized by these different forms, and to get the percentages of the different growth-forms in the flora. For the purpose of comparison he established a "normal spectrum" which is constructed on purely hypothetical lines. It consists of 400 species carefully chosen from 1,000 representative species. The analysis of these 400 species into their different growth-forms gives, theoretically, the ideal phytoclimatic spectrum of the whole earth. According to Raunkiaer the percentage of species belonging to each growth-form, in the ideal spectrum of 400 species, is as follows:

PERCENTAGE OF GROWTH-FORMS IN NORMAL SPECTRUM[4]

Type of growth-form.....	MG & MS	MC	N	CH	H	G	HH	T
Percentage of growth-forms.....	6	17	20	9	27	3	1	13

These percentages are supposed to reflect the average condition as to the growth-forms of the whole earth. Of course they may need future revision; it would be strange if they did not as our knowledge of the habits of various species increases.

The method of comparing the climate of different parts of the earth's surface, on this conception, involves working out the percentages of the different growth-forms exhibited in the areas and a

[4] I have omitted epiphytes and stem-succulents, as being two of Raunkiaer's groups hardly applicable to our area.

comparison of the figures thus obtained. The following table gives a few of the percentages as determined by Raunkiaer for widely separated areas. The percentages of the normal spectrum are given for comparison.

PERCENTAGES OF GROWTH FORMS IN BIOLOGICAL SPECTRA, AFTER RAUNKAIER

Type of Growth-form	MG and MS	MC	N	CH	H	G	HH	T
Normal spectrum	6	17	20	9	27	3	1	13
Baffin's Land			1	30	51	13	3	2
Georgia	5	7	11	4	55	4	6	8
Denmark	1	3	3	3	50	11	11	18
Seychelles	10	23	24	6	12	3	2	16
Libyan Desert		3	9	21	20	4	1	42

These figures give some idea of the variation of climate implied by the different growth-forms predominating in the different areas. They also make more cogent the terms phanerophytic, hemicryptophytic and chamaephytic as applied to climate.

Raunkiaer has indicated three types of climate, as shown by his study of growth-forms, namely a tropical area, an area of decreasing warmth correlated with an increasing difference between winter and summer temperatures and with a favorable distribution of precipitation, and lastly a region with decidedly decreasing temperature, or also, very commonly, with an unfavorable distribution of precipitation, such as in deserts. The tropics are typical of the first of these conditions, the eastern sides of North America and Asia are typical of the second, and the arctic region and some deserts are characteristic of the third type of climate, which may be seen also in our own Southwest. Many refinements of these rather gross outlines of climate have been worked out, based on the so-called biochore, which is a line with the same percentages of a definite growth-form, as found in different parts of the continent. Such a study of the flora of North America would be extremely interesting. It can be rightly based only on complete percentages of growth-forms for different parts of the country, and it is with the idea of supplying this for the local flora area that the present paper has been written.

In attempting to apply Raunkiaer's principles described above and to get the biological spectrum of the flora near New York, I have thrown out of the calculation all the 615 species of introduced weeds,

the 85 ferns and their allies, and 24 parasites. This leaves 1,907 native species that are found, roughly speaking, within 100 miles of New York City. Each species has been put in one or other of the categories mentioned above with the following result.

BIOLOGICAL SPECTRUM OF THE FLORA OF NEW YORK AND VICINITY[5]

Growth-form	MG	MS	MC	N	CH	H	G	HH	T
Gymnosperms.....		15	2	2					
Monocotyledons....			5		53	197	202	164	57
Dicotyledons.....	10	62	130	65	48	438	195	60	191
Totals.....	10	77	137	67	101	635	397	224	248
	%	%	%	%	%	%	%	%	%
Percentages of growth-forms.....	.52	4.03	7.18	3.51	5.29	33.29	20.23	11.74	13

The most remarkable figure in this list is the high percentage of geophytes, 20.23 per cent. For no region in the world has there been published such a large percentage of these plants with bulbs, rhizomes, corms and other subterranean methods of winter protection. Among the 692 native monocotyledons in the area, over 29 per cent are geophytes, while for 1,200 native dicotyledons there are only 16 per cent of the same growth-form. Undoubtedly the high percentage of monocotyledons in our flora, the pine-barrens of New Jersey are especially rich in them, has much to do with the large percentage of geophytes. Most of the regions with high geophyte percentages are arctic or sub-arctic; and, from this point of view, the high geophyte percentage in our area is misleading and it may be a response to quite other factors than climatic ones. As compared to the percentages of the normal spectrum those for the local flora are higher in the case of the aquatics, geophytes, and hemicryptophytes, lower in the case of chamaephytes and all the phanerophytes, and the same in the percentage of annuals.

Figures for other countries, mostly northern, show for hemicryptophytes averages ranging from 50 per cent to 60 per cent, the local flora percentage is only 33.29 per cent, well illustrating the condition that prevails in our area, where only a moderately large number of species are of northern origin. The percentage of all phanerophytes in our area is about 14.88, in the normal spectrum it is 43

[5] Not counting .57 per cent of stem-succulents.

per cent, in the Seychelles it is 57 per cent. Upon Raunkiaer's assumption that phanerophytes are typical of warm and tropical regions the figures of the local flora are somewhere near what one would expect.

In the flora of New York and vicinity 13 per cent of the wild species are southern plants reaching their northern distribution outposts in the area within 100 miles of the city. We should expect to find these southern plants exhibiting a greater percentage of growth-forms characteristic of the warmer parts of the earth, than of those characteristic of the north. In this same area, also, 8 per cent of the native plants are typically northern and reach their southern distribution outposts in the region within about one hundred miles of the city. We should expect to find the percentages of growth-forms characteristic of the north predominating in these northern species. The following table gives the percentages of growth-forms in the southern species, the northern species, and, for comparison, the percentages in the whole native flora. The normal spectrum is included again, for comparison.

PERCENTAGES OF GROWTH-FORMS IN THE NORTHERN AND SOUTHERN SPECIES OF THE FLORA OF N. Y. AND VICINITY THAT REACH THEIR DISTRIBUTION OUTPOSTS IN THE AREA

	MG	MS	MC	N	CH	H	G	HH	T
Normal spectrum...	6		17	20	9	27	3	1	13
Whole native flora..	.52	4.03	7.18	3.51	5.29	33.29	20.23	11.74	13
Southern species....		5.62	7.08		7.83	30.97	20.53	7.83	14.92
Northern species....		1.31	3.94	8.55	8.55	26.31	24.34	23	3.94

There are, of course, hundreds of northern and southern species that range north or south of the local flora area,[6] but it seemed best to ignore these, and consider only those that find either their southerly or northerly distribution outposts within the region.

An analysis of these percentages of northern and southern species shows that the main lines of Raunkiaer's scheme are admirably illus-

[6] The area included is as follows: All of the State of Connecticut; in New York the counties bordering the Hudson River up to and including Columbia and Greene also Sullivan and Delaware counties, and all of Long Island; all of New Jersey; and in Pennsylvania, Pike, Wayne, Monroe, Lackawanna, Luzerne, Northampton, Lehigh, Carbon, Berks, Bucks, Schuylkill, Montgomery, Philadelphia, Delaware and Chester counties.

trated in the local flora. We find in the southern species about 12 per cent shrubs or trees, in the northern species only 5 per cent, well illustrating the tendency for the woody plants to increase in size and profusion as we travel southward. Among the small undershrubs there appear to be none in the southern group, but over 8 per cent in the northern, which is considerably over the percentage for this growth-form in the whole flora. One of the most notable elements is the large percentage of HH in the northern species (23 per cent) and the large percentage of geophytes in the same group (24 per cent). Both these figures are so much above those published for any other region, that they may be open to the suspicion that other than climatic factors have influenced them. This region in eastern North America has never had this particular criterion of temperature response applied to it, in fact I know of no region where such a large number of species as our 1907 native plants have been used in making up the percentages as published by Raunkiaer, Vahl, and Paulsen for other countries. On the basis of the large numbers of species considered, and the obviously temperate nature of our climate, it may be that the normal spectrum as now understood is in need of revision. Certainly it seems to be much too low in the case of geophytes and the aquatics, and too high in the microphanerophytes.

There are 19 northern species in the area, reaching their southerly distribution outposts here, but found only at elevations in excess of 1,000 ft., and most closely approximating an alpine habitat of any of our native plants. Of course, percentages of growth-forms based on such a small number of species are apt to be misleading, but as illustrating a tendency they prove interesting. The following is a list of such species:

GROWTH-FORMS OF NORTHERN SPECIES REACHING THEIR SOUTHERLY DISTRIBUTION OUTPOSTS IN THE AREA, BUT FOUND ONLY AT ELEVATIONS IN EXCESS OF 1000 FT.

Xyris montana = H
Juncus filiformis = G
Spiranthes Romanzoffiana = G
Mitella nuda = H
Fragaria canadensis = CH
Fragaria terra-novae = CH
Rubus pergratus = H
Pyrus sitchensis = MS
Viola nephrophylla = G
Viola Selkirkii = G
Viola renifolia = G
Moneses uniflora = G
Ledum groenlandicum = N
Vaccinium Brittonii = N
Adoxa Moschatellina = G
Valeriana uliginosa = G
Solidago macrophylla = H
Aster junceus = H
Petasites palmatus = H

PERCENTAGE OF GROWTH-FORMS IN ABOVE LIST

(The percentages of the whole region included for comparison)

Growth-form	MG	MS	MC	N	CH	H	G	HH	T
Whole region.....	.52	4.03	7.18	3.51	5.29	33.29	20.23	11.74	13
Northern mountain species.....		5.26		10.52	10.52	31.57	42.1		

In the case of mesophanerophytes the percentage is obviously misleading, but the notable figure here, as in all those for the local flora area, is the high percentage of geophytes. It is often difficult to decide whether or no any given species belongs to the geophytes or hemicryptophytes, but errors of assignment to one or other of these groups should about equalize each other. It cannot be, then, that this abnormally high geophyte percentage is even partially explainable upon the assumption that many plants are incorrectly credited to the group, as there is no more reason why they should have been incorrectly assigned to this group than to any other.

The conclusion as to the climate of our area, as reflected in the spectrum of the whole flora is that the conditions seem more favorable here for the production of deep-rooted perennials of the bulb-bearing or rootstock type than any region as yet studied, and that the production of aquatics is relatively great. Figures for eastern Asia in this connection would be of interest. Such generalizations must mean very little as yet, because all such schemes of correlating climate and plant distribution deal with species rather than individuals. Biological spectra based on a census of individuals would very greatly alter the result. The chief value of this scheme of Raunkiaer's, and it is the most suggestive of all schemes yet devised for the purpose, is the opportunity it gives for comparison of one flora with another, for comparing certain elements of the same flora, and it has been used in studying even smaller categories of vegetation. To the ecologist and phytogeographer it opens up a wide field of investigation. Its value to the practical agriculturist and horticulturist must be apparent, as it can be applied as a criterion of hardiness and suitability of plants from one region for another. A study of the scheme from this standpoint would surely reveal much information of value to growers.

In the following four families, as illustrating the method, the species have been assigned to their respective growth-forms. In many cases it is not easy to assign the species, and much valuable work can be

done along this line. It would be of the greatest service to know all the growth-forms as shown in certain areas, formations, associations and so forth.

IRIDACEAE

Iris versicolor = G
Iris primsatica = G
Sisyrinchium angustifolium = H
Sisyrinchium mucronatum = H
Sisyrinchium arenicola = H
Sisyrinchium gramineum = H
Sisyrinchium atlanticum = H

ALSINACEAE

Stellaria uliginosa = T
Stellaria pubera = H
Stellaria longifolia = T
Stellaria borealis = T
Cerastium nutans = T
Cerastium arvense = H
Cerastium arvense oblongifolium = CH
Sagina procumbens = T or biennial?
Arenaria caroliniana = CH
Arenaria stricta = CH
Arenaria groenlandica = CH
Arenaria lateriflora = H
Arenaria peploides, Spergularia marina } = stem succulents

ROSACEAE

Physocarpus opulifolius = MC
Spiraea latifolia = N
Spiraea alba = N
Spiraea tomentosa = CH?
Gillenia trifoliata = G
Potentilla pumila = H
Potentilla canadensis = H
Potentilla canadensis simplex = G
Potentilla monspeliensis = T
Potentilla arguta = H
Potentilla palustris = CH
Potentilla tridentata = CH
Potentilla fruticosa = N
Fragaria vesca americana = CH
Fragaria virginiana = CH
Fragaria canadensis = CH
Fragaria terrae-novae = CH
Sanguisorba canadensis = H
Agrimonia gryposepala = H
Agrimonia rostellata = H
Agrimonia mollis = H
Agrimonia Bicknellii = H
Agrimonia striata = H
Agrimonia parviflora = H
Geum vernum = H
Geum virginianum = H
Geum canadense = H
Geum flavum = H
Geum strictum = H
Geum rivale = H
Waldsteinia fragarioides = H
Rubus 28 species all H
Rosa 7 species all N

HYPERICACEAE

Ascyrum stans = CH
Ascyrum hypericoides = CH
Hypericum Ascyron = H
Hypericum densiflorum = N
Hypericum adpressum = CH
Hypericum Bissellii = G
Hypericum ellipticum = G
Hypericum virgatum = G
Hypericum perforatum = G
Hypericum punctatum = G
Hypericum mutilum = T
Hypericum gymnanthum = T
Hypericum majus T?, Hypericum canadense T? } perhaps biennial
Hypericum gentianoides = T
Hypericum virginicum = T